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Conservation of data deficient species under multiple threats: Lessons from an iconic tropical butterfly (*Teinopalpus aureus*)

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ABSTRACT

With increasing pressure from wildlife trade, conservation efforts must balance deficiencies in distribution data for species (the Wallacean shortfall) with the risk of increasing accessibility of locality for collectors. The Golden Kaiser-I-Hind (*Teinopalpus aureus* Mell) is an iconic butterfly restricted to Southeast Asia, popular in trade markets but lacking in ecological and conservation information. We compiled occurrence records and used them to assess multiple threats of *T. aureus* distribution-wide and at the national level. Results of species distribution models suggest that suitable habitats of *T. aureus* are montane forests in mid to high elevations in Southern China, Laos and Vietnam. However, habitat networks for the species are poorly connected, with some portions of its distribution experiencing intensive deforestation and threatened by climate change. The trade assessment results showed specimens of *T. aureus* were available for sale with high prices, indicating potential pressure from trade markets. We also found different conservation statuses and efforts to protect *T. aureus* across countries; the species is under strict protection in China, moderate protection in Vietnam and has no protection in Laos. Both recorded locations and projected distribution in the three countries were poorly covered by protected areas. These results together demonstrate the importance of distribution data in conservation management of threatened species while highlighting trade-offs inherent in not making location information widely available when trade pressure is present. Finally, we strongly encourage cross-border cooperation in sharing ecological information for consistent conservation management of species under multiple threats from habitat loss, climate change and illegal wildlife trade.

1. Introduction

The paucity of geographic information, or the Wallacean shortfall, has been demonstrated to be one of the biggest challenges in conservation biogeography (Lomolino, 2004; Whittaker et al., 2005). This shortfall impedes the assessment of conservation status for information-limited species and could lead to missing conservation opportunities for rare species under multiple threats (Brooks et al., 2006; Samways et al., 2010; Schuldt and Assmann, 2010; Cardoso et al., 2011a). While there is an urgent need to understand the distribution of threatened species, the sharing of locality information to the public, without risk evaluation, can cause further disturbance or exploitation of trade-threatened species (Lindenmayer and Scheele, 2017; Tulloch et al., 2018). As such, the need for providing species distribution information for ecological research and conservation intervention must be balanced with the need for restriction in releasing location information for species under risk of exploitation (Ocampo-Peñuela et al., 2016; Tulloch et al., 2018).

Across the globe, a significant biodiversity information gap has been identified in subtropical and tropical Asia, with a large proportion of data deficiency in species georeferenced records (Collen et al., 2008; Meyer et al., 2015; Li et al., 2016). Meanwhile, poaching for wildlife trade has caused severe conservation problems in this region, and has been identified as one of the primary drivers of recent population declines and species extinctions (Sodhi et al., 2004; Nijman, 2010;

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Wilcove et al., 2013; Harrison et al., 2016). While caution is needed when releasing locality information to avoid overexploitation for species in demand by trade markets, there is also an urgency to make distribution information available for research and conservation of species that are facing additional threats including habitat loss and climate change (Sodhi et al., 2004; Wilcove et al., 2013; Corlett, 2014; Hughes, 2017). Tropical forests have experienced severe logging impacts and land-use changes in recent decades (Hansen et al., 2013; Song et al., 2018). Southeast Asia, in particular, continues to suffer among the highest deforestation rates globally (Sodhi et al., 2004; Hansen et al., 2013; Wilcove et al., 2013). Additionally, a rapidly changing climate has heavily impacted this region by driving species range shifts and redistributions (Chen et al., 2009; Freeman and Freeman, 2014; Cheng et al., 2018). Given that protecting species from single threats typically fails to achieve conservation goals (Mora et al., 2007; Hughes, 2017; Symes et al., 2018a, b), integrating the impacts of multiple anthropogenic threats is essential in assessing species extinction risk as well as making conservation recommendations (Brook et al., 2008; Sirami et al., 2017).

Naturally, the distribution of a species depends on its biological traits, biotic interactions and environmental factors, but is rarely limited by political boundaries such as national borders (Huffman and Wallace, 2012). The major threats faced by different populations within species may, however, vary between political units through differences in management and development strategies as well as social and cultural influences. Meanwhile, legislative systems and environmental policies could further mediate threats to species within political boundaries (Dallimer and Strange, 2015). Therefore, the conservation status of a given species may vary across countries, which may consequently affect both the current and future distributions of the species. While most species conservation studies are country-based, ecological data collection and studies at regional and global scales are likely to be more effective in conservation (Schuldt and Assmann, 2010).

Despite their high diversity and importance for conservation, insects are in general poorly studied and protected in tropical Asia, but are threatened by habitat loss and disturbance, and likely to experience significant geographic range losses with warming impacts (Bonebrake et al., 2016; Rossetti et al., 2017; Warren et al., 2018). In addition, the popularity of insect collection for specimen trade and a lack of relevant policy interventions may accelerate the decline and extinction of insects (New, 2005; Courchamp et al., 2006). However, the lack of basic biological and ecological information limits the ability to assess conservation status and identify the main threats to most insect species (Diniz-Filho et al., 2010). At the species level, targeted insect conservation efforts are particularly rare in the tropics (Bonebrake et al., 2010). To date, there are very few studies integrating distribution information and ecological knowledge together with conservation policies and social-economic concern of species across different countries to estimate multiple threats, and conservation status for threatened insect species. Species distribution models (SDMs) can not only assist in understanding specific environmental requirements for targeted species, but also have the potential to mask the actual locations of trade-sensitive species (Tulloch et al., 2018), thus making for a useful tool in assessing the vulnerability of threatened but data deficient insect species (Buse et al., 2007; Cardoso et al., 2011b; Miličić et al., 2017; Bosso et al., 2018; Guareschi et al., 2018; Jenkins et al., 2018).

The Golden Kaiser-I-Hind (*Teinopalpus aureus* Mell) is a butterfly species restricted to high elevations in South China, Vietnam and Laos (Morita, 1998; Masui, 1999; Igarashi, 2001). With its striking appearance and relative rarity in the wild, it has been proposed as the national butterfly and is under the strictest conservation protection within China (Huang et al., 2015). However, it is also a popular butterfly species in trade markets for specimen collection (Li et al., 2013). Previous field-based studies of *T. aureus* in China have found that it is sensitive to environmental temperature and that habitat loss and fragmentation could be major threats to the species (Zeng et al., 2012; Wang et al., 2018). Potentially facing multiple threats, the extinction risk of *T. aureus* has not been assessed yet; its current conservation status is data deficient on the IUCN Red List of Threatened Species due to a lack of population and distribution information (Collins and Morris, 1985; Gimenez Dixon, 1996).

In this study, by collecting occurrence records of *T. aureus* across different countries, we aim to 1) understand the suitable habitats of the species to further estimate its global distribution; 2) assess the vulnerability of the species under multiple pressures; and 3) evaluate and compare the current effectiveness of conservation efforts by different countries in protecting the species. Besides providing the latest distribution information for the understanding of threats for an improved species-specific conservation action plan for *T. aureus*, we also use this example as a case study to evaluate the risk of publishing georeferenced information for determining the best strategy for releasing distribution information to enhance the research and conservation of species under multiple threats.

2. Materials and methods

2.1. Ecological information

The basic life history of *T. aureus* has been studied in some parts of its distribution in China. *T. aureus* is active during the wet season from April to October and spends the dry season as pupae (Lin et al., 2017). The species is typically bivoltine with the first generation active from April to June and the second from July to September. The major host plant is *Michelia foveolata*, but the larvae can also feed on plants belonging to multiple genera of family Magnoliaceae including *Michelia*, *Manglietia* and *Magnolia* (Jia et al., 2014).

2.2. Collection and summary of location information

The recorded locations of *T. aureus* for China, Vietnam and Laos were collected from a variety of sources, including published information in scientific publications, museum specimen records, field observations (Table A1), as well as personal communication from other lepidopterists in Laos (Steeve Collard, pers. comm., 2017). In total, we gathered 59 occurrence localities where *T. aureus* has been recorded since it was first described by Mell (1923). Among those locations, 36 locations were recorded in China, 19 in Vietnam and 4 in Laos. No obvious clustering was evident in the locations, most of which are at least 10 km from each other while only two locations are within 1 km, thus minimizing possible spatial autocorrelation effects. We collated these records from July to August 2017.

We summarized the climatic conditions of the recorded locations by downloading monthly mean precipitation, monthly mean temperature, monthly mean maximum temperature and monthly mean minimum temperature at the 30 arc-second resolution from WorldClim ($0.93 \times 0.93\,\text{km} = 0.86\,\text{km}^2$ at the equator) (Hijmans et al., 2005) where *T. aureus* had been recorded. We then summarized each of the climatic variables across the 59 locations where *T. aureus* have been recorded over the year and during the period when the butterflies are active from April to October (Zeng et al., 2012; Lin et al., 2017).

2.3. Distribution modeling

We downloaded 19 bioclimatic variables at the 30 arc-second resolution from WorldClim version 1.4 (Hijmans et al., 2005) and then checked the collinearity of all 19 environmental variables using the *vif* function in the *usdm* package (R v 1.1-15, Naimi, 2015) and eventually chose eight bioclimatic variables with vif < 10 (Table A2) for species distribution modeling as recommended by Guisan et al. (2017). For future climates, we used the downscaled IPCC5 data for the chosen eight bioclimatic variables. We applied three general circulation models (GCMs): HadGEM2-AO (Bellouin et al., 2011), IPSL-CM5A-LR (Dufresne

et al., 2013) and MRI-CGCM3 (Yukimoto et al., 2012) at the 30 arc-second resolution. We used two extreme representative concentration pathways (RCPs), RCP2.6 and RCP8.5 for future distribution projections in 2070 with climate change. RCP 2.6 represents an optimistic scenario with greenhouse gas (GHG) emissions peaking around 2010–2020 and declining afterwards, while RCP 8.5 represents the most severe scenario with GHG emissions continuously rising throughout the 21st century (IPCC, 2014).

We conducted the species distribution modeling to estimate the current and future distributions for *T. aureus* using the *biomod2* package (R.v.3.3-7, Thuiller et al., 2016). Based on occurrence information depicting species presence only, we randomly generated a matching number of pseudo-absence locations as recommended by Barbet-Massin et al. (2012). We employed eight algorithms by methods commonly used for establishing the relationships between species presence and climatic variables (Hamid et al., 2018; Smeraldo et al., 2018; Miller et al., 2018) provided in *biomod2* package (R.v.3.3-7, Thuiller et al., 2016). These algorithms comprise regression-based approaches including generalized linear models (GLMs) and multiple adaptive regression splines (MARS); classification approaches and machine learning systems including classification tree analysis (CTA), flexible discriminant analysis (FDA), and artificial neural networks (ANNs); envelope approach such as surface range envelope (SRE); boosting and bootstrap aggregation methods including generalized boosted models (GBM) and random forest (RF) (Guisan et al., 2017). We set the same weight for presence and pseudo-absence data for distribution modeling. We used 70% of the occurrence data to calibrate the models and the remaining 30% for model evaluation. We evaluated the performance of the eight models over 3 pseudo-absence sampling runs with 10 cross-validation runs by threshold dependent and independent tests including true skill statistic (TSS) and the area under the curve (AUC) of the relative operating characteristic (ROC) (Fielding and Bell, 1997; Allouche et al., 2006; Guisan et al., 2017; Eaton et al., 2018).

As previous field studies have suggested that the occurrence of *T. aureus* is highly associated with well-preserved evergreen broadleaf forest and mixed broadleaf-conifer forest (Zeng et al., 2012), we refined our current and future distribution maps to areas with forest cover information including evergreen/deciduous needleleaf trees, evergreen broadleaf trees, deciduous broadleaf trees, and mixed/other trees from Tuanmu and Jetz (2014). In this way, the projected suitable habitat takes both climate suitability and habitat type into account. We produced the final ensemble binary distribution maps of species absence and presence using the TSS method based on models with a TSS > 0.8 and AUC above 0.7 to project habitat suitability for *T. aureus* (Coetzee et al., 2009; Araújo et al., 2005; Guisan et al., 2017; Smeraldo et al., 2018). We also calculated and compared the change in habitat suitability between future climate change scenarios and current projections across the three countries. We produced the habitat suitability change map based on such calculations for each of the GCM predictions in both RCP 2.6 and RCP 8.5 scenarios in 2070.

We further quantified climate change threats to *T. aureus* across countries for two extreme scenarios depending on the ability of the species to disperse and colonize a new site based on the produced binary distribution map. We first calculated the estimated elevational shifts as the full dispersal scenario assuming the species could track its suitable climate without limitation in dispersal ability. The predicted elevational shifts were quantified by averaging the elevation of both projected current and future distributions of *T. aureus*, and then subtracting the future averaged elevations by the current elevations. We also estimated the percentage of suitable distribution range loss that *T. aureus* will experience for the non-dispersal scenario which assumed the species ability to disperse and colonize a new location is highly restricted by non-climatic factors and will be constrained within its current distribution. The percentage of predicted suitable distribution range loss was calculated by dividing the number of grids the species occupies in future climate change scenarios remaining within its current distribution range by the number of grids in its current distribution range. We averaged the value over all grids within each country for each GCM projection under RCP 2.6 and RCP 8.5 scenarios for comparison and calculated the mean results with standard deviation across three GCM projections.

2.4. Forest loss assessment

We used the high-resolution map ($30 * 30$ m) of global forest cover loss by Hansen et al. (2013) spanning 2000 to 2015 to quantify the experienced forest cover loss within the suitable habitat range for *T. aureus*. We calculated the average proportion of forest loss across grids in each country based on the final ensemble binary distribution map. We resampled $30 * 30$ m grids at $900 * 900$ m resolution and calculated forest loss as the proportion of $30 * 30$ m grids that exhibited forest loss as a proxy for the intensity of forest loss at $900 * 900$ resolution. We then produced the forest loss map to visualize forest loss intensity within the suitable distribution range for *T. aureus*.

2.5. Trade assessment

To evaluate the market availability of *T. aureus*, we gathered trade information from Convention on International Trade of Endangered Species (CITES) records and online markets. As all three countries (China, Laos and Vietnam) have ratified CITES, all international trade of the species should be recorded by CITES. We therefore searched the CITES database of the recorded international legal trade for this species from 1975 to 2018. We also collected information on the species posted for sale from one internationally popular e-commerce platform to understand what may affect the price of the products of the species. We decided not to disclose the name and link of the surveyed platform for ethical reasons, following common practice for online trade market survey studies (Martin et al., 2018; Sung and Fong, 2018). We searched the species posted by entering "*Teinopalpus aureus*" in the search bar. We chose to search by the scientific name of the species to avoid potential language bias in our sampling. For each post, we collected information including price and origin. When the picture of a specimen for sale was available, we also retrieved the sex of the specimen. We aimed to record all *T. aureus* specimens presented on the platform during each survey and included new ones when added. Therefore, we established an accumulated database that contains all items listed for sale during our online sampling period. We conducted monthly surveys of the platform from December 2017 to August 2018. As we only sampled one single platform in a relatively short period, the origins and quantity of specimens in our results may not represent the actual scope and scale of the entire trade market of *T. aureus*. In addition, the platform we used may not share the same popularity across countries. For instance, domestic retail websites are most commonly used within China and physical markets are more prevalent and accessible in Laos. We therefore also searched two main domestic online retail websites in China using both the scientific name and the Chinese name "金斑喙凤蝶", but found no results, possibly due to the strict protection level of the species in China (see below).

We then tested if sex and origin affect the price of the specimens based on collected retail information following similar approaches in recent related studies (Purcell, 2014; Sung and Fong, 2018). We applied a multiple linear regression model with price as the response variable, and sex (three levels: female, male, and unidentified) and origin (five levels: China, North Vietnam, Central Vietnam, South Vietnam, and unidentified regions in Vietnam) as well as their interactions as categorical factors. As the price was not normally distributed, we used log-transformed price as the response in the model. We conducted the multiple linear regression model using the function *lm* in R v. 3.3.3 (R Core Team, 2017).

2.6. Evaluation of conservation efforts across countries

We evaluated and compared the conservation efforts of different countries towards *T. aureus* using two approaches. First, we compared the conservation status and the relevant management policies of the species in each country. To this end, we collected information from national laws on biodiversity regarding the status of *T. aureus* in each of its three countries of occurrence (New, 2008; Gärdenfors, 2001). Secondly, we conducted a gap analysis by calculating the percentage of the documented locations and projected suitable distributions of *T. aureus* within protected areas in each country to compare the national level effectiveness of protected areas (Scott et al., 1993; Chape et al., 2005). For this purpose, we first downloaded a protected area layer from the World Database on Protected Areas (WDPA) from the Protected Planet website (https://www.protectedplanet.net/). We then overlaid this layer with both species occurrence records and the suitability distribution map and separately calculated the percentage of occurrence and suitable habitat covered by protected areas (Cheng and Bonebrake, 2017). When overlaid with the suitable distribution map, we also calculated the coverage for future climate change scenarios to evaluate the effectiveness of protected areas in protecting *T. aureus* with climate change impacts, similar to approaches used in Cheng and Bonebrake (2017) and Cianfrani et al. (2018).

2.7. Assessing the risk of publishing location information

We applied the decision tree by Tulloch et al. (2018) for the location information releasing of *T. aureus* based on existing background information and our results. We assessed each step in a relatively conservative way due to the limited information on population size and trends to fully evaluate the overharvesting risk of the species (Fig. A1).

3. Results

3.1. Current distribution of T. aureus

Based on the climate conditions among the locations where *T. aureus* has been recorded, we found that the butterfly prefers to inhabit relatively cool and humid mid-high elevations in Southern China, Laos, and Vietnam. The air temperatures extracted from occurrence records ranged from 12.96 °C to 20.71 °C, with an annual mean air temperature of 16.84 °C and monthly mean precipitation of 149.10 mm (Table A3). The climatic conditions during the butterfly active period were slightly warmer and more humid compared with that of the whole year (Table A3). Recorded elevation ranged from 439.42 m to 1905.85 m with 1010.84 m as the mean.

The habitat suitability map from SDMs showed that southern China may provide the largest suitable areas for *T. aureus* and that some areas in northern Laos and Vietnam are also suitable (Fig. 1). The predicted current suitable habitats are, however, exhibiting high levels of fragmentation and little connectivity over the entire suitable distribution (Fig. 1). The projected average elevation of the current suitable habitat distribution ranges from 813.75 m to 1280.27 m in each country with 1085.15 m as the mean across countries.

3.2. Projected changes in distribution

With climate change, habitat suitability within most of the current estimated distribution will severely decrease as predicted by the three GCM models for both RCP 2.6 and RCP 8.5 scenarios in 2070 (Fig. 2). Under full dispersal scenarios (assuming *T. aureus* can colonize any location without biological limitations), the species will need to shift 140.21–554.34 m upwards to track its suitable habitat with appropriate climate and forest types under two RCP scenarios in different countries. Under non-dispersal scenarios, there would be a loss of 76.93% on average ranging between 53.59% and 96.87% (depending on the scenario) of current suitable habitat within the three countries under different climate change scenarios (Table 1).

3.3. Forest loss in recent decades experienced by T. aureus

The level of forest loss varied across countries. The most severe forest loss experienced by the species occurred in Laos, where about 8.99% of the projected suitable distribution of *T. aureus* experienced forest cover loss from 2000 to 2015, and the areas of forest loss seem to be most severe and intense in northern Laos near the border with Vietnam (Fig. 3). Similarly, 8.65% of its distribution in China showed forest cover loss, while the loss pattern seems to be more evenly distributed across the projected distribution of *T. aureus*. In Vietnam, 8.28% of the projected distribution showed forest cover loss, mostly in southern Vietnam (Fig. 3).

3.4. Market availability

We only found two recorded cases from CITES for international transactions of *T. aureus*, separately in 2006 and 2008. Both of the records were exported from Vietnam (one through Germany) and were exported to the US (Table A4). However, we recorded 189 items in total that were either sold (n = 60) or labelled for sale (n = 129, and 102 of them have been once removed during our sampling) on the sampled e-commerce platform over an 8-month survey period, with 34 females, 109 males and 46 specimens for which sex was not available (already sold, hereafter referred to as data deficient) (Fig. A2). All specimens were sold by 4 vendor accounts, with 62% from one vendor.

There was a large variance of price recorded for the posted specimens, ranging from 1.3 USD to 700.4 USD, with the 68.77 USD as the average. Sex and origin, but not their interaction, significantly affected the price of the specimens in the sampled platform ($F_{11,172} = 25.61$, $p < 0.001$, $R^2 = 0.60$, Sex: $F = 124.58$, $p < 0.001$, Origin: $F = 5.63$, $p < 0.001$, Sex∗Origin: $F = 2.00$, $p = 0.08$, Fig. 4). Females have significantly higher prices than males (Fig. 4). In addition, during our sampling, we noticed one alleged hybrid between *Teinopalpus aureus* and *Teinopalpus imperialis* listed for sale at 1234 USD.

3.5. Conservation efforts across countries

Conservation status and protection levels varied greatly from one country to another (Table 2). The lowest level of protection is in Laos, where *T. aureus* is not listed as a species of conservation concern, therefore belonging by default to "common or general species". This is perhaps because only some vertebrates are classified under the "prohibition category" or "management category", according to the Wildlife and Aquatic law (2006) (Table 2). In China, *T. aureus* is listed as a Class I species (the highest protection level, and only 2 terrestrial invertebrates species are included in this category at present) since 1989 and is protected by "Law of the People's Republic of China on the Protection of Wildlife Order 44-46" and "Criminal law Order 341" (Table 2). Violation of such laws and poaching 3–5 individuals would result in a 5 to 10 years sentence in prison, if > 6 individuals, the sentence could be > 10 years. In Vietnam, according to the Decree 32/2006/ND-CP (2006) on the Management of Endangered, Precious, and Rare Forest Fauna and Flora Species, *T. aureus* is classified under the Endangered species category IIB, which makes it illegal to collect or possess this species unless a permit has been provided (usually through the Forest Protection Department) (Table 2).

Among the 59 locations where *T. aureus* had been documented, only 42.45% of the locations occur within protected areas at the national level. While the percentage under protection was around 50% for both China and Vietnam, only one of the four (25%) documented locations were within protected areas in Laos (Table 3). For the projected current distribution, only 10.05% is covered by national level protected areas in China, while 28.01% of the suitable distribution is protected within

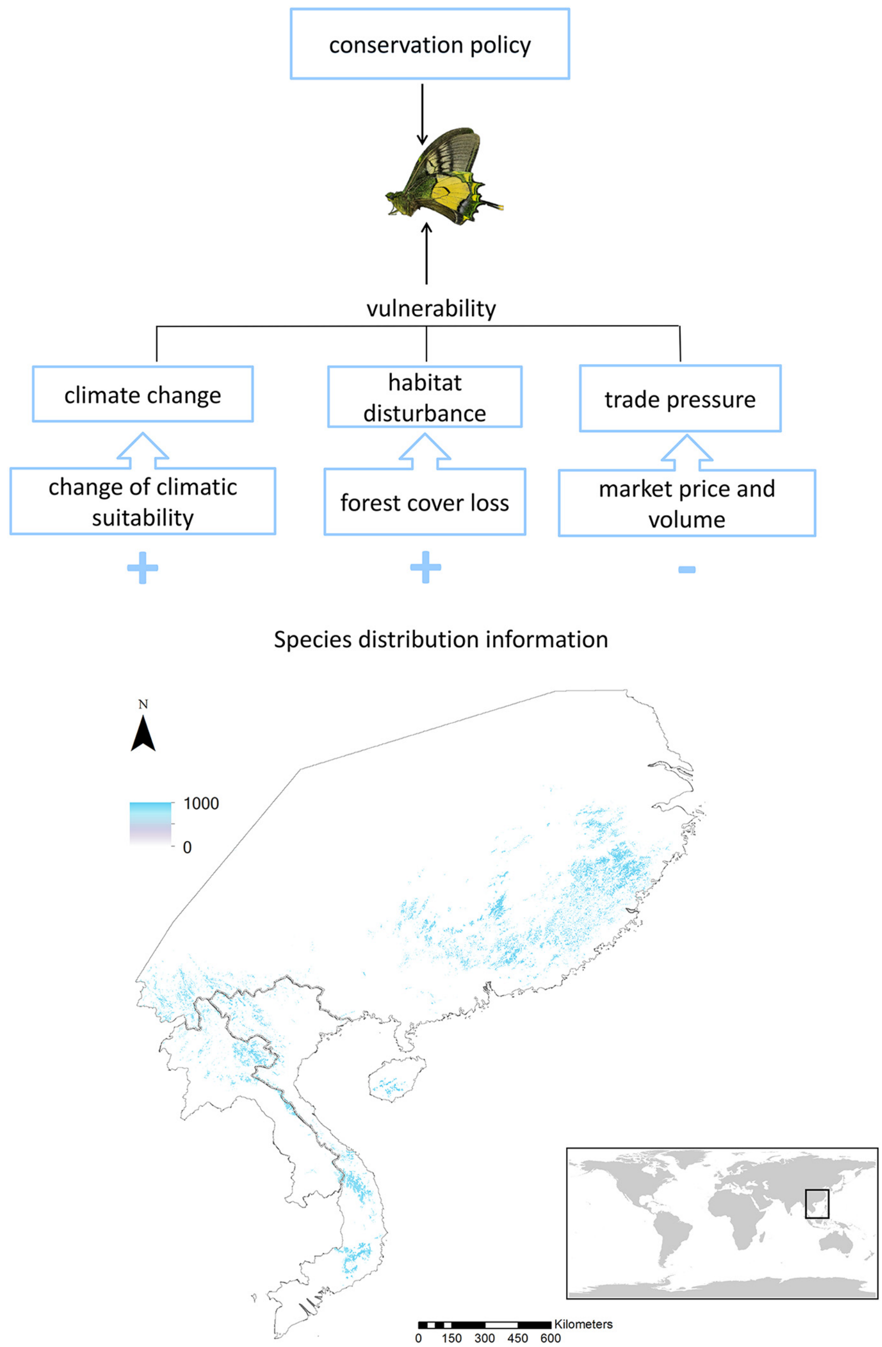

Fig. 1. Framework of assessing the vulnerability of *T. aureus* (the plus and minus symbol indicate the potential positive and negative effects of releasing species distribution information for understanding and mitigating the three proposed threats) together with estimated suitable habitat across regions where *T. aureus* has been recorded (blue end indicates higher suitability while white end indicates lower suitability). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Vietnam and 32.76% in Laos. With climate change, the proportion of distributions covering the protected areas tends to slightly increase in general, but the protected proportion would still be less than half of the suitable distribution areas within each country (Table 3).

3.6. Releasing distribution information

Following the decision tree designed by Tulloch et al. (2018), we decided to publish the high- resolution habitat suitability map instead of releasing the locality information due to the potential threats of exploitation and human disturbance (Fig. A1). We therefore provided the predicted distribution map by the SDMs for future study and conservation planning of *T. aureus* (Fig. 1).

4. Discussion

By focusing on the lack of information and conservation concerns of a tropical butterfly species *T. aureus*, we emphasize the urgent need to collect basic ecological information for data deficient species with critical cultural value currently facing multiple threats. Additionally, our results highlight the necessity of comparing the threats and environmental policies across borders for species distributed in multiple countries. We also applied a recently published decision tree (Tulloch et al., 2018) to evaluate the potential of overharvesting risk when

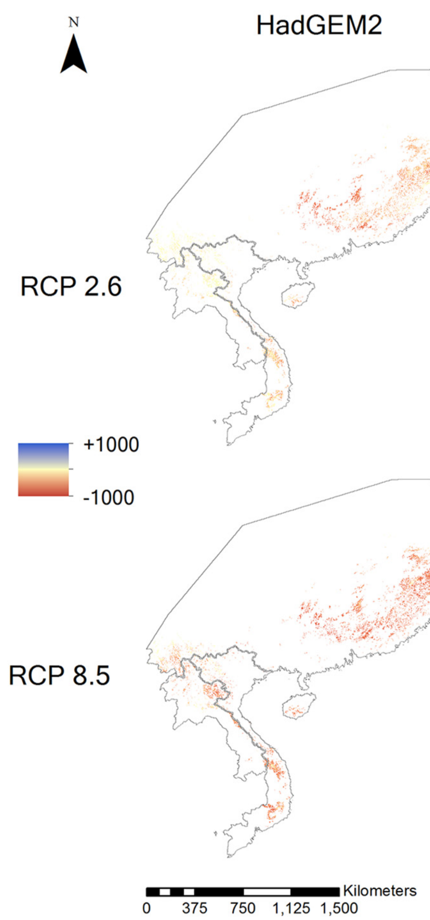

Fig. 2. Predicted change of habitat suitability with different climate change scenarios by different GCM models in 2070. Blue suggests increase in habitat suitability while red suggests decrease in habitat suitability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Estimated upwards range shift and suitable habitat loss (mean ± standard deviation) of *T. aureus* with climate change in 2070 under different climate change scenarios in three countries.

Country	Elevational shift (m)		Habitat loss (%)	
	RCP2.6	RCP8.5	RCP2.6	RCP8.5
China	206.82 ± 295.98	509.43 ± 408.77	62.59 ± 18.72	88.81 ± 12.86
Laos	140.21 ± 55.58	387.43 ± 48.12	71.62 ± 22.13	96.87 ± 4.21
Vietnam	231.06 ± 89.52	554.34 ± 116.27	53.59 ± 13.04	88.07 ± 1.92

releasing distribution information. High resolution distribution maps without locality information (but based upon such data) could be useful for further distribution exploration but could also mask location information to avoid additional species harvest, especially when the species are not strictly protected over their entire distributions. Finally, we recommend more cross-boundary collaborations in both ecological research and conservation to protect threatened species and support regional biodiversity.

4.1. Climate change impacts

We found *T. aureus* to be generally restricted to mid-high elevation ranges across subtropical and tropical Asia that share relatively cool and narrow temperature niches. Zeng et al. (2012) recorded that male *T. aureus* stopped hill-topping when environmental temperatures exceeded 26 °C, suggesting that its reproductive activities could be sensitive to high temperatures. Furthermore, our SDM results suggest that with climate change by 2070, *T. aureus* will lose the majority of its current suitable habitats within each of the distributed countries based on different warming scenarios. The species would have to shift up over a hundred meters to track its suitable climatic conditions. Such predictions are consistent with the general pattern that tropical species may have narrow breadths of thermal tolerance and elevational bands that challenges their ability to cope with novel thermal regimes induced by climate change (Janzen, 1967; Deutsch et al., 2008). As a species restricted to high elevations, the availability of land area for *T. aureus* to move into might be limited in a warmer world (Colwell et al., 2008).

4.2. Forest loss

Besides climate change threats, we found that on average > 5% of forest cover had been lost within the distribution of *T. aureus* across all three countries from 2000 to 2015. Habitat loss and fragmentation have been increasing threats to biodiversity and ecosystems in subtropical

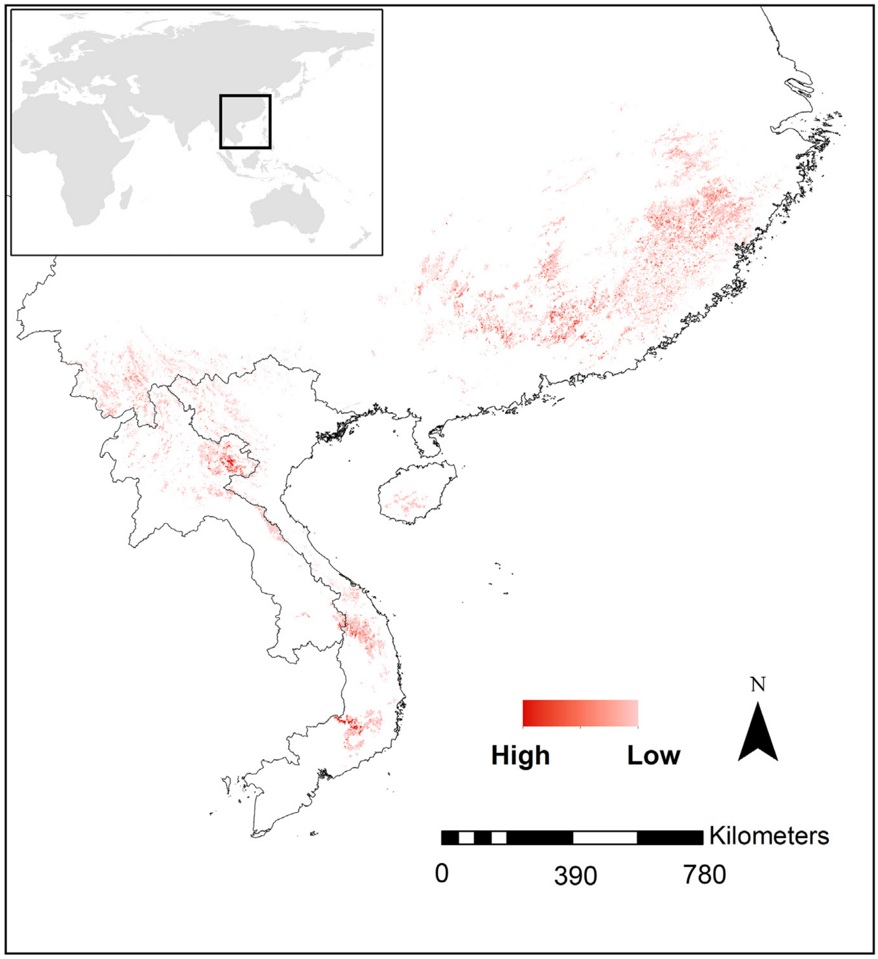

Fig. 3. Observed forest cover loss from 2000 to 2015 within the projected current distribution of *T. aureus*. Darker red color indicates higher intensity of forest cover loss. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and tropical Asia (Rudel et al., 2009). Although butterflies do not require large habitats to thrive, they could be sensitive to habitat loss and have shown high extinction rates under deforestation impacts at local scales in this region (Brook et al., 2003; Vu and Yuan, 2003). Additionally, forest specialist species with relatively narrow ecological niches could face high extinction risk with deforestation through the loss of host plants, and may not be able to adapt to disturbed habitats (Hamer et al., 1997; Koh et al., 2004a; Koh et al., 2004b; Bonebrake et al., 2010). One study in China has shown that *T. aureus* can be abundant at local scales in suitable habitats with a high availability of host plants and recommended protecting suitable habitat to be the conservation priority for the species (Wang et al., 2018).

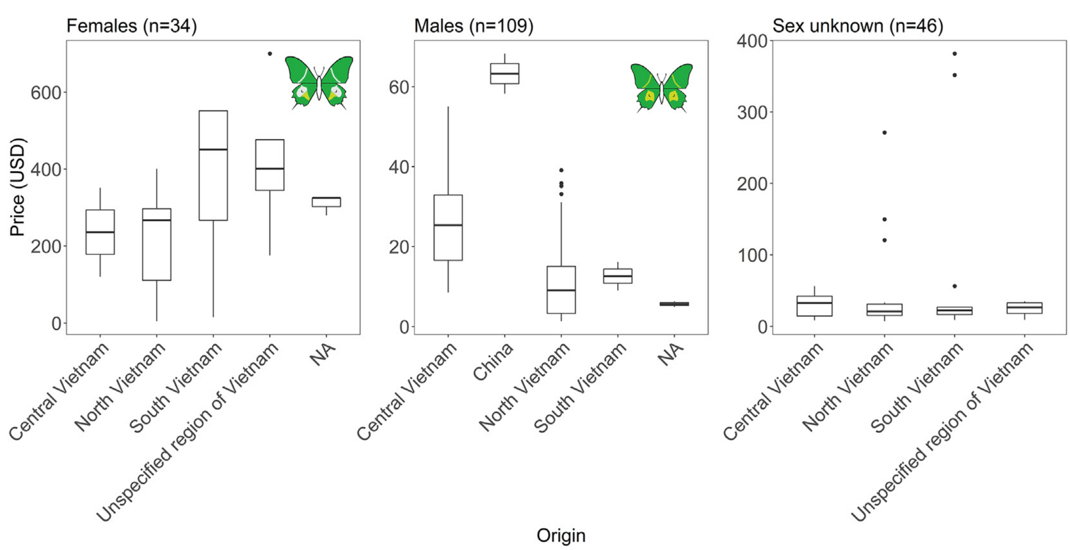

Fig. 4. Boxplot of price and origins of *T. aureus* specimens for different sexes.

Table 2
Comparison of current conservation status and policies of three countries in protecting *T. aureus*.

Country	Conservation status	Possession	Collection	Trading
China	Class I (highest level)	Only when authorized by the state council of PRC	Only when authorized by the state council of PRC	Only when authorized by the state council of PRC
Laos	Common and general category (lowest level)	No restriction	Allowed when no harm to population, permit required; Not allowed within core zones of national protected areas	Legal for business use and breeding with authorization
Vietnam	Endangered species category IIB (medium level)	Only with license (with the origin declared and transport license)	Only allowed for scientific use, permit required, either inside or outside protected areas	Legal for scientific purposes and for international cooperation with authorization

Table 3
Coverage of protected area for documented occurrence and projected current and future distribution (mean ± standard deviation) of *T. aureus* in each country (PA = protected area).

Country	Number of locations within PA	Percentage of locations within PA (%)	Percentage of distribution within PA with climate change (%)		
			Current	RCP2.6	RCP8.5
China	16	44	10.05	12.48 ± 1.12	27.15 ± 14.80
Laos	1	25	32.76	42.30 ± 16.32	34.98 ± 29.28
Vietnam	11	56	28.01	28.49 ± 1.01	32.61 ± 5.33

Furthermore, the synergistic effects of habitat loss and climate change will likely be a challenge for habitat-specialist insects such as *T. aureus*, which require cohesive habitat networks with availability of host plants to keep colonizing within suitable climate niches (Opdam and Wascher, 2004; Brook et al., 2008; Fourcade et al., 2017). The projected current distribution of *T. aureus* reflects that habitats with suitable forest types and climatic conditions are already highly fragmented and disconnected across the region, and most of the sites are becoming less suitable for the species with climate change. As such, populations of *T. aureus* may be more isolated with a reduction in habitat size, and may consequently face higher extinction risk with limited dispersal ability (Wilcox and Murphy, 1985). In addition, habitat loss and human disturbance in low elevations may further restrict the distribution of *T. aureus* on mountain tops. In a global-scale analysis, Guo et al. (2018) revealed that upward shifts of species could be a compounded consequence of both climate change and habitat loss in lowland habitats, suggesting that high elevation habitats are critical refuges for biodiversity. With its striking appearance, cultural value and popularity, *T. aureus* is of high conservation interest and could be valued as a flagship species for high elevation tropical invertebrates that may share similar habitats and are threatened by common anthropogenic pressures in subtropical and tropical Asia (New, 2011; Barua et al., 2012; Wang et al., 2018).

4.3. Trade market

While only two incidents of the international trade of *T. aureus* have been recorded by CITES in the past few decades, we found high numbers of *T. aureus* sold or posted for sale based on our online market survey. We noticed significant differences in quantity and price between sexes of specimens posted, with fewer females, but labelled at much higher prices than males. It is not known yet what may be the cause in the difference of prices between sexes. This could be a consequence of the cost of harvest effort per individual as females are relatively inactive and hard to spot compared to males in the wild, although an almost 1:1 sex ratio has been observed in previous rearing experiments (Wang et al., 2018). Such high prices posted for female specimens, may, however, stimulate further collection of the species from the wild.

We observed that volume and price of posted specimens also varied across stated origins the vender provided, with the majority of specimens for sale originating from Vietnam. Currently, *T. aureus* is under the highest protection level in China against species harvesting and trade, which are only allowed for scientific purposes when authorized by the state council of PRC. Likewise, the species could only be allowed to be collected and traded for research purposes with permits in Vietnam. Nonetheless, the specimens of *T. aureus* that are labelled as originating from both countries are found available for sale in this internationally popular e-commerce platform, indicating that illegal harvesting and trading is likely taking place.

So far, relatively few studies have investigated and monitored the insect trade market compared to other groups (Slone et al., 1997; New, 2005), thus the impacts of overexploitation on insect populations is

unclear, and no evidence has shown that overexploitation alone can cause insect species extinction (Slone et al., 1997; Wang et al., 2018). Our knowledge of overharvesting effects on insects is limited by the challenges in quantifying harvesting effort and monitoring population dynamics, as well as difficulties in untangling different factors attributed to population declines (Mora et al., 2007; Hopping et al., 2018). Experimental studies have also demonstrated that overharvesting may reduce the resistance of populations to habitat degradation and rapid warming effects (Mora et al., 2007). Case studies investigating the trade and harvest of caterpillar fungus (*Ophiocordyceps sinensis*) based on local ecological knowledge have suggested overexploitation could be an important cause of population decline in the Himalayas (Shrestha and Bawa, 2013; Hopping et al., 2018). The excessive and intensive collecting activities have also been considered as one of the causes of butterfly decline in Japan, which can have large local impacts on threatened species (Nakamura, 2011). For this reason, the availability of the species for sale and the high price for female specimens on e-commerce platforms should be a concern for the conservation of *T. aureus*, and the market availability and trading of the species should thus be continuously monitored in the future.

Butterfly ranching and farming could be a viable conservation strategy which could regulate the exploitation of valuable butterflies and also bring economic benefits to local communities (Slone et al., 1997; Boppré and Vane-Wright, 2012; Sands and New, 2013; Vereecken, 2018). Such approaches have been proposed for *T. aureus* by Li et al. (2013) considering the increasing knowledge on the life history of the species. In a recent study, Wang et al. (2018) assessed the feasibility of breeding *T. aureus* in captivity and showed it to be difficult, and therefore advised against captive breeding as a conservation strategy for this species. To our knowledge, *T. aureus* is not being farmed anywhere at the moment. In particular, the strict protection level may also make its permitted captive breeding extremely difficult (even for research purposes) within China. The harvest and trading of rare butterfly species (including CITES-listed species) in large amounts have been observed within a protected area in Vietnam and such activity could potentially occur in Laos and China as well (Vu and Yuan, 2003). Considering the fact that captive breeding is currently not available and species-targeted collection with decent volumes and high prices are popular in this region, we suggest that increasing access to the species locations could consequently increase overharvesting threats for certain populations. Cross-border monitoring of trade markets and interventions of species collection should be a conservation priority and laws should be enforced for *T. aureus* as well as other popularly traded insect species from the wild (New, 2005).

4.4. Conservation management for tropical butterflies

The conservation of *T. aureus* suffers from similar problems with many other conspicuous and valuable tropical butterfly species (New et al., 1995). First, there is very limited ecological information for the majority of tropical butterfly species due to the shortage of relevant studies (Bonebrake et al., 2010; Sands and New, 2013). Likewise, species-specific conservation management is rare as major threats to species are poorly known and conservation resources are relatively limited in the tropics (New et al., 1995; Bonebrake et al., 2010). Secondly, the trade of insects in general has lacked attention and is in need of more effective monitoring and regulation (New, 2005; Vereecken, 2018). Lastly, protected areas tend to fail targets to protect butterfly species in many regions (Thomas, 2016).

Species-specific management and conservation projects have been applied to some iconic tropical butterfly species. In order to save Queen Alexandra's Birdwing (*Ornithoptera alexandrae*), a highly distribution-restricted and market demanded species in Papua New Guinea, conservation efforts have focused on promoting the species as a flagship species to protect the rainforest, improving the conservation awareness and providing economic and social incentives for local communities (New, 2007). Another comprehensive butterfly conservation project is the Richmond Birdwing Conservation Project for the Richmond birdwing butterfly (*Ornithoptera richmondia*) in subtropical Australia, which involves multiple conservation approaches including the preservation of rainforest, building and improvement of habitat connectivity, cultivation of food plants, control of invasive exotic weeds, conducting thorough ecological research, community engagement and sharing of conservation networks (Sands, 2008; Sands and New, 2013). These projects require intensive conservation investment with continuous management efforts and long-term effectiveness of those conservation practices need to be assured and monitored. However, such projects have advanced butterfly conservation significantly and provided valuable knowledge and experience which could be applicable to other threatened butterfly species such as *T. aureus* (Wang et al., 2018).

4.5. Implications for cross-border conservation

The global habitat suitability projection for this data-deficient species enabled us to evaluate and compare the vulnerability of different populations across each political unit based on potential threats and present conservation efforts. Valued as the national butterfly of China, *T. aureus* is under the highest national protection level, the same as the giant panda (*Ailuropoda melanoleuca*), and the penalty and enforcement of law appear strong and effective in protecting the species against poaching threats (Li et al., 2013; Wang et al., 2018). However, more than half of the species occurrences and most suitable habitats were outside the national level protected areas in China (Table 3), which have also experienced large areas of forest loss in the past decade (Fig. 3). In Vietnam, *T. aureus* is also rated as an endangered species and is under a moderate level of protection, where the hunting and trading of the species are under regulation (Table 2). In Laos there is currently a paucity of conservation concern for the species and its natural forest habitats has been rapidly lost within some parts of the projected suitable habitat (Fig. 3). The variance in conservation policies regarding the collection, possession and trading of *T. aureus* harvesting in the three countries may lead to different vulnerabilities of populations across its distribution. While the cultural significance of the species may influence its conservation status in different parts of its range, social, economic and political factors might also contribute to the inconsistency of species conservation across countries (O'Connor et al., 2003; Symes et al., 2018a, b). The current data-deficient status of *T. aureus* may further limit the conservation effectiveness at both regional and international levels, the product of a failure to share ecological data and coordinate cross-border conservation efforts. Such conservation challenges are more likely to be a general issue particularly in developing regions such as Southeast Asia, where high biodiversity is coupled with limited conservation resources to cope with multiple global change impacts (Sodhi et al., 2010; Corlett, 2014).

Considering the multiple threats *T. aureus* faces across the three countries, cross-border conservation efforts are necessary. We recommend the initialization of a cross-border protection network that aims to establish climate change refuges for *T. aureus* and potentially other vulnerable tropical insects living in high elevation forests in Southeast Asia. We also recommend establishing coordination mechanisms for population information, conservation status designation and protection intensity between countries to reach consistent conservation management at the regional or international level. In addition, the establishment of a conservation network with community engagement that could be shared across countries would improve the regional awareness in species conservation. Finally, we encourage the sharing of illegal trade information and collaboration between different enforcement units together with e-commerce and social media platforms to combat illegal wildlife trade. These cross-border conservation plans should be considered as conservation priorities for maintaining regional species diversity under global change impacts.

4.6. Conclusion

By presenting the first global distribution map for a data deficient, regionally endemic and globally iconic tropical butterfly species, this study has revealed the multiple threats that tropical insects are facing, and the inconsistency of conservation policies across boundaries for a single species. Although there is an urgent need to share distribution information for enhancing ecological knowledge and species conservation, the market availability of the species raised the concern that further access may increase the harvesting pressures on *T. aureus*. For this reason, we suggest the need for treading the Wallacean shortfall carefully for this species and other high profile invertebrates. Here we propose the use of releasing high resolution suitability habitat maps as a practical strategy for species with high market availability and prices. While general conservation management and protected networks can be effective when conserving overall biodiversity and ecosystems, species-specific conservation plans will be particularly important for species under multiple stresses. Future cross-boundary conservation collaboration and coordination would bring great benefit for protecting regional and global biodiversity from anthropogenic impacts.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.03.029.

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